Vivipary in Phormium

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INTRODUCTION.

Vivipary is rare in the New Zealand flora, the mangrove providing the only example which comes within Goebel's definition (1905) of "continuous development of the seed, without a resting period." The term is often used, however, for want of a better, to cover the substitution of vegetative for sexual buds giving rise to that curious condition, familiar in *Agave,* where young plantlets are seen to spring full-fledged from the flowering panicle. In *Agave americana* substitution may be complete for the whole panicle, and the sturdy plantlets, stored with food reserves, are called **bulbils.** They are capable of independent growth after a short time, and have in fact become the normal method of reproduction for the species. In grasses, particularly those of wet habitats (e.g., Yorkshire Fog and *Poa bulbosa)* the bulbils may replace the whole, or part, of a spikelet. With regard to such grasses, and many members of the rush family, the only general conclusion seems to be that this vegetative switch-over occurs most in high latitudes and at high altitudes, mainly outside the height of the flowering season.

The observations we have made on partial vivipary in a native genus, *Phormium,* now advanced by Hutchinson (1934) from the *Liliaceae* to the *Agavaceae,* do not solve what Goebel, Nannfelt and others have left unexplained, but they seem worthy of setting down as a record of as pretty a case of physiological disturbance as any yet published.

Briefly, *Phormium* bulbils differ from those of *Agave* in that they do not fall of their own "ripeness"; they have little or no food reserve and yet may grow independently once aerial root-rudiments appear; and if they remain attached to the scape they may very soon have a sexual phase, thus short-circuiting the four-year cycle which is about the minimum necessary to bring seedlings into flower.

Early Records: Two examples of aberrant behaviour have been described from coastal populations of *colensoi* and *tenax,* and a third is reported below. Of the first two, both from the Taranaki coast, one was briefly noted by Walsh (1882, *tenax)* and another by Williams (1904, *colensoi).* From seed of the latter Williams raised a plant that also developed "leafy bracts" over several years. Cheeseman (1925) referring to this account states that a plant growing in his garden (apparently obtained from Bishop Williams) "produced these leafy bracts, many of which were eighteen inches long, for four or five years in succession, but in one year only did flowers appear as well."

Viviparous plants were next discovered by Mr. A. J. Healy very near the sea at Wellington, and were examined by the senior author on the 30th July, 1937. Normal plants everywhere at that date bore scapes, mainly with all capsules and bracts fallen. The viviparous scapes were fresh and green, the lower branchlets bearing the remains of abortive or unfertilised flowers, without bracts. The upper branchlet sets were crowded together and each densely clad in small fans of leaves, more or less enclosed within green bracts (Pl. 52, fig. 4). These fans (hereafter spoken of as vivipars) averaged five leaves ranging from 1 to 7 dm. long. Some had short stout aerial rootlets, while some had short secondary scapes up to 3 dm. long, each bearing a few branchlets, the lower with tiny vivipars, some dead, the upper with small flowers, some at early anthesis, some with immature capsules, and a few with well-developed but small capsules. Some capsules had dehisced. Mature capsules reached up to 8 cm., were erect and only slightly twisted, and were thus very distinct from those of normal *P. colensoi,* though the vegetative parts were very similar.

Cultivated examples came to our notice in 1932, and as the early records did not give a very clear picture of the phenomenon, breeding tests were begun soon after in an attempt to clear up the situation. However, changes of residence by both authors, and damage by stock, prevented our carrying the investigations as far as we might have wished.

THE PARENT PLANTS.

Our breeding work was done on two plants in Auckland, one at the Diocesan High School (S) and the other in the garden of the late Sir A. P. W. Thomas (T). As far as we can ascertain, both of these are descendants of the plant cultivated by Bishop Williams, T, at least, according to its grower, having been cut from a scape over 30 years before. S, now destroyed because of its "ugly" habit, grew in loose garden soil rich in humus, and formed a large spreading bush (Pl. 52, fig. 3). In September, 1932, it carried about a dozen green scapes of different ages, each with a bushy head from 2 to 4.5 dm. across, and from 2 to 9 dm. long. The largest had weighed down its scape almost to the ground, and some of the vivipars had developed roots, some of which plunged deeply, while others had only loose contact with the soil. Rhizome development had begun in some cases. Only one secondary scape was seen (Text fig. 1) and from its one capsule 6 out of 9 seeds were later germinated, but in November and December other little scapes appeared on this and other viviparous heads. These scapes resembled those noted above for wild plants, normal flowers usually producing an abundance of nectar and of apparently good pollen. Most of the flowers dropped off, but a few developed capsules and good seed before the scapes shrivelled. As time went on it was seen that the appearance and flowering of these scapes was quite irregular: although commonest in early December, they matured in August, September, May and June, as well, often with abnormal flowers. The more vigorous vivipars grew firm fans of leaves, not scapes. If roots developed strongly, even in mid-air, these plantlets could be removed and planted out successfully. No vivipar showed any tendency to drop off.

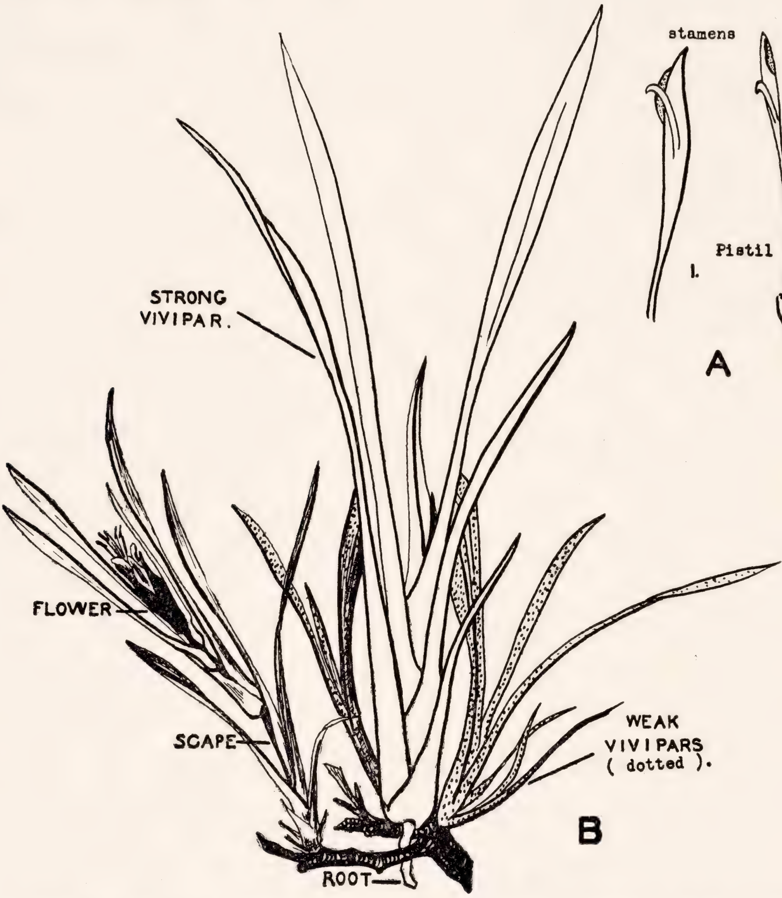

Fig. 1. A: (1) foliaceous stamen; (2) doubled pistil with modified stamen on left. B: rough sketch of branchlet cut from scape, showing strong vivipar with root, failing vivipars around it, and small vivipar bearing a single flower on a **secondary scape.** Specimens from Diocesan parent plant.

New primary scapes developed each year in January and February, the normal flowering time, their flowers maturing more rapidly than those on the secondary scapes. Flowers, both normal and abnormal, appeared on lower and vivipars on upper parts of each scape. Long persistent bracts enclosed all sets, the development of the flowers often being checked by them, many rotting inside, or falling away when freed. Yet many capsules set seed under open pollination.

Plant T, growing in the shade on a lateritic soil derived from basalt, behaved in the same way, but the vivipars were less strongly developed.

Flowering of Vivipar Transplants: In the following all observations refer to the plants grown at Palmerston North, unless otherwise stated. Portions of the Diocesan parent plant grown since 1932 at Henderson both on poor clay and on alluvial soil were equally erratic in behaviour; small rooted vivipars secured at the same time established slowly in the latter soil, and flowered on lax scapes for the first time in 1940, while many of the seedlings planted out in 1933 and 1934 grew rapidly and came into

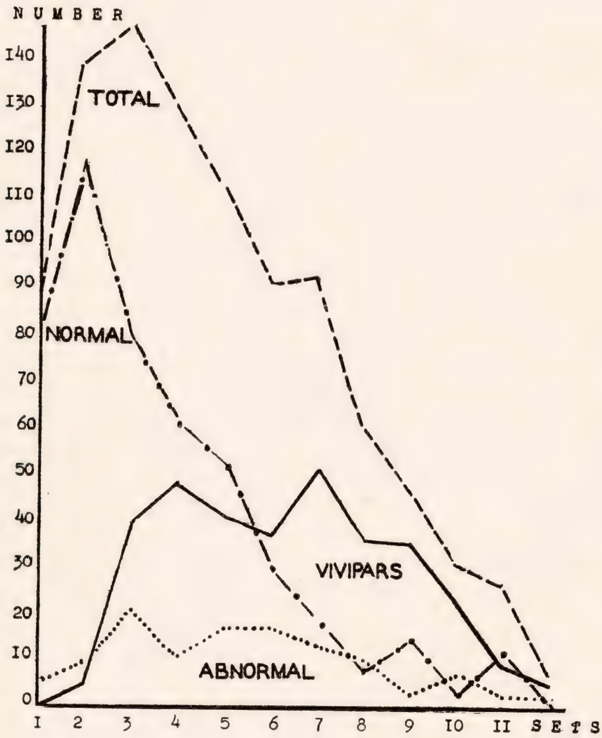

Fig. 2. Graph showing distribution of normal and abnormal flowers, and of vivipars, in each set up to the 12th bract.

flower within about four years of germination. Calves destroyed or damaged so many of these young plants that it was thought better to confine detailed observations to the Palmerston North material.

THE PROGENY.

Artificial pollination was effected between 5/12/32 and 14/12/32. Certain plants received *tenax* pollen from Auckland Domain, the rest pollen from the parent plant. Capsules from open pollinated flowers were also gathered from T. From S seven capsules were secured on 20/2/33, and the seed was sown on 26/4/33. Germination was observed from 26/6/33. In some capsules (e.g., No. 4) very few seeds were properly developed.

Capsules.	Pollen.	Seeds.	Seedlings.	Planted out.
1	*tenax*	41	6	5
2	,,	1*	1	1†
3	self	26	20	15
4	,,	18§	6	5
5	,,	12	2	1
6	,,	60	30	20
7	,,	8	5	2

*Rest shed. †Accidentally destroyed. §40 Imperfect.

From T 175 seedlings were obtained. Planting out was done on 18/4/34. On 4/6/34 there were transplanted to the Plant Research Bureau grounds, Palmerston North, 12 plants from capsule 6, two from capsule 4, together with 60 from T. The plantlets remained almost at a standstill till the late spring, and 11 died. From then on there was a steady growth. Certain of the plants sent up scapes in January, 1937, and the plot (Plate 52, fig. 1) was studied from 7/2/37 to 10/2/37. For help in this we are indebted to Mr. A. L. Poole, of the Botany Division of the Bureau. The two plants from capsule 4 were still rather weak, the one with leaves 6 dm. long and 9 small fans, the other with leaves 5 dm. long and 5 small fans. Of the twelve plants from capsule 6, nine survived, two bearing scapes. Of the T plants 51 survived, of which 11 bore one or more scapes. Details are given in the following tables.

SCAPE-BEARING PLANTS.

Series Number.	Dimensions of Plant in Metres. Height.	Spread.	Dimensions of Leaves in Centimetres. Length.	Width.	Number.	Scapes Length in Metres. Basal Part.	Inflorescence Part.	Angle of Emergence.
10	1.6	2	114.5	7	2	2.2	1	80°
						2	.9	45°
11	1.4	1.9	142	7.6	1	1.8	1.2	45°
13	1.1	1.4	90	6.7	1	1.8	.9	40°
16	1.6	1.9	120	6.4	2	2	1	40°
						2	1.1	40°
18	1.6	1.8	112.5	7.4	2	2	1	45°
						1.8	1	40°
22	1.4	2	120	7.4	1	1.7	1.1	45°
23	1.4	1.8	100.5	7.6	1	1.5	1	55°
25	1.8	2.5	124.5	8	4	1.9	1	45°
						1.6	.9	45°
						1.9	.9	45°
						1.8	1	45°
27	1.6	2	128.5	7.9	2	1.5	.7	45°
						2.2	.9	45°
36	1.4	1.8	131	6.7	3	2	1.1	45°
						2	1	50°
						2	1	75°
37	1.8	2	48	3.8	1	2.1	1	60°
39	1.7	2.25	114	8.1	3	2.3	1.1	50°
						2.1	.8	60°
						2	.9	45°
53	2.8	3.5	189	8.8	3	2.3	1.7	80°
						4.25	1.6	75°
						2.2	1.9	80°
Average	1.6	2.1	118	7.2	2	2	1	52°

At the time of examination the tendency to an increase of vivipars among the upper sets was already noticeable, while in the individual sets the tendency was for the lower flowers to be replaced by vivipars. The bracts, more strongly developed than on normal inflorescences, hindered, and in several cases completely prevented, the development of the flowers and even of the vivipars on the enclosed branchlets. This was especially striking on plant 16. All plants on the plot were measured, and averaged: height 1.4 m., spread 1.8 m., leaf-length 110 cm., leaf-breadth (at widest part) 6.7 cm. The scape-bearing plants showed, therefore, rather greater vigour than the non-flowering plants. Accepting volume as a measure of vigour, it will be seen that in general the plants more vigorous vegetatively were also more vigorous sexually, e.g., plants 25, 39 as contrasted with 23, 13. Exceptions are the vegetatively vigorous 37 with only one scape, and the vegetatively weak 36, with three scapes.

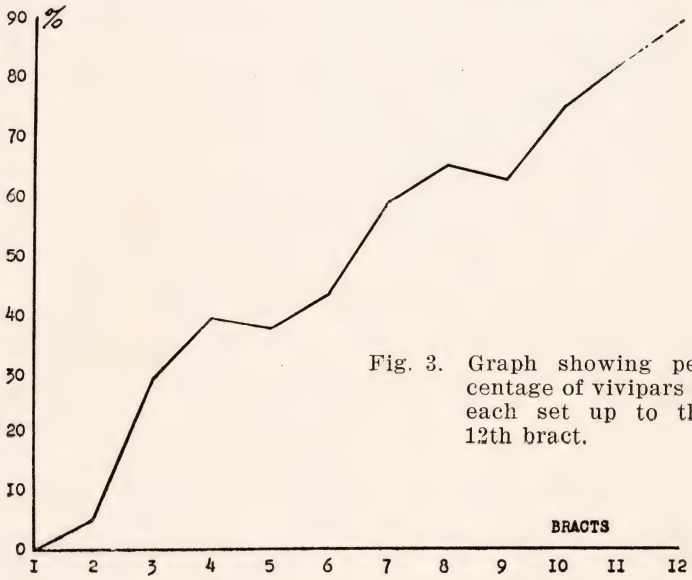

Fig. 3. Graph showing percentage of vivipars in each set up to the 12th bract.

Plant 53 (Plate 52, fig. 1), obtained under open pollination. is remarkable for its great size and tall, well-developed, semi-erect scapes bearing practically normal inflorescences. The leaves are almost as erect as in *P. tenax,* with red margins and split tips. An analysis of one scape showed at bract 1: bract dying, branchlets with all flowers fallen; at bract 2: bract fallen, branchlets carrying 21 capsules and 51 flowers on bare pedicels; at bract 3: bract fallen, 25 capsules, 29 fallen flowers; at bracts 4 to 11: bracts fallen, branchlet numbers decreasing, all carrying one or more flowers still at anthesis. The whole scape carried 163 maturing capsules, which were about 10 cm. long, horizontal, slightly curving upwards, bluntly trigonous and slightly twisted. The capsules strongly resembled those borne on artificial *colensoi* x *tenax* hybrids (Allan and Zotov, 1937). Capsules on the other plants were also intermediate in appearance, though usually more twisted (Plate 52, fig. 2).

DESCRIPTION OF PLATE 52.

Fig. 1. General view of plot of viviparous offspring in first year of flowering. Note range in size. The large scapes belong to No. 53, a vigorous hybrid closest to *tenax*, which has shed most of its bracts and has an almost normal inflorescence.

Fig. 2. Smaller plants, one with the drooping *colensoi* scape, another with a congested scape bearing strong bracts and semi-trigonous, slightly twisted capsules.
For these two photographs, taken on 8/2/37, we are indebted to Mr. Harvey Drake.

Fig. 3. Habit of parent plant (S) at Diocesan School, 1932; three bushy heads are shown on the left. Photo L.M.C.

Fig. 4. Primary scape of one of the wild plants found at Wellington by A. J. Healy in 1937; vivipars probably more than one year old. Photo H. Drake.

Eight scapes were analysed in detail:—

ANALYSIS OF SELECTED SCAPES.

N = Normal flowers or swelling capsules.
A = Abnormal flowers.
V = Vivipars.
? = Material decomposed.

Set	Plant	10A	10B	22	23	36A	36B	36C	39A	Total.	Grand Total.
1	N	1	20	3	13	20	15	14	0	86	
	A	0	6	0	0	0	0	0	0	6	92
	V	0	0	0	0	0	0	0	0	0	
2	N	28	19	4	7	21	21	23	0	123	
	A	0	6	4	0	0	0	1	0	11	141
	V	0	0	2	3	1	0	1	0	7	
3	N	16	1	6	12	22	15	11	2	85	
	A	4	9	1	0	0	0	1	5	20	146
	V	0	3	2	9	11	1	5	10	41	
4	N	12	2	7	11	14	12	8	0	66	
	A	6	0	1	0	2	2	1	2	14	130
	V	1	3	1	4	10	0	19	12	50	
5	N	9	0	3	9	12	8	14	0	55	
	A	5	1	1	4	2	1	0	5	19	117
	V	0	5	6	4	7	0	11	10	43	
6	N	4	1	2	1	5	7	13	0	33	
	A	4	6	0	4	0	3	1	1	19	92
	V	5	8	0	6	2	0	2	17	40	
7	N	6	0	2	3	3	6	2	0	22	
	A	5	2	0	0	2	1	3	2	15	93
	V	1	9	5	13	3	0	11	14	56	
8	N	?	0	1	2	3	1	3	0	10	
	A	?	1	0	1	0	2	1	6	11	60
	V	?	7	2	9	3	3	8	7	39	
9	N	?	0	0	2	3	11	2	0	18	
	A	?	0	0	1	0	1	0	2	4	59
	V	?	9	2	4	5	5	6	6	37	
10	N	?	0	0	0	0	1	2	0	3	
	A	?	0	0	3	0	0	0	2	5	31
	V	?	4	2	0	1	5	5	6	23	
11	N	?	?	0	1	?	12	0	0	13	
	A	?	?	0	1	?	1	0	0	2	27
	V	?	?	1	3	?	0	3	5	12	
12	N	?	?	0	0	?	?	?	0	0	
	A	?	?	0	1	?	?	?	0	1	7
	V	?	?	1	3	?	?	?	2	6	
Totals—											
	N	76	43	28	61	103	109	92	2	514	
	A	24	31	7	15	6	11	8	25	127	995
	V	7	48	24	58	43	14	71	89	354	
		107	122	59	134	152	134	171	116	995	

Thus of a total of 995 units counted from 8 scapes, 514 were apparently normal, 127 had modified stamens, pistils or both, and 354 had become fully vegetative.

The nature and distribution of the abnormal flowers is shown in the table below:—

Bract	1	2	3	4	5	6	7	8	9	10	11	12	Total
♂	2	4	12	3	8	3	6	7	1	2	—	—	48
♀	4	6	7	10	7	12	8	3	1	2	2	1	63
♂ + ♀	0	1	1	1	4	4	1	1	2	1	—	—	16
Total	6	11	20	14	19	19	15	11	4	5	2	1	127

Thus 64 were affected in the androecium and 79 in the gynaecium, with the greatest development of abnormality in the mid sets. As these sets contain the greater number of flowers in general, there does not appear to be any significant relation between abnormality and position in the scape. Nor does there appear to be any particular trend towards a special form of abnormality either in general or according to position in the scape. Abnormal flowers are very occasional in wild plants, mainly in the terminal florets of a set, and the aberrant features are those shown by the viviparous plants. In the latter, however, they are much more frequent and show more extreme development. The perianth parts may be increased or decreased in numbers, and show different degrees of concrescence, sometimes becoming almost free (Text fig. 1). The stamens may be more or fewer than six, and show a range of tepaloid forms, from a simple expansion of the filament with a normal anther to a completely tepaloid structure lacking any sign of an anther. The gynaecium shows a distinct tendency to doubling, the two pistils being completely separated or joined to different degrees, while they may be of equal or of very different size.

While the strong tendency to abnormality in the flowers appears to be associated in its causes with that to vivipary, we have seen no indication that an abnormal flower is in any way tending towards becoming a vivipar. The vivipars appear to develop from vegetative buds that have entirely replaced flower-buds. The capsule characters are such as are found in hybrids (diversity in the progeny suggesting that the *colensoi* parents, like Healy's, may not be pure), but it has to be remembered that the young ovary of *colensoi* is definitely trigonous, and in view of the flower abnormalities shown by the viviparous plants, it is possible that the semi-trigonous and less twisted capsules formed by them are not always due to hybridism.

Some inflorescences carried more than twelve bracts and sets of branchlets, but it was not found possible to analyse these satisfactorily. The percentage of vivipars on the different scapes works out at 39, 41, 43, 28, 11, 42, 77 (not including the rather meagre analysis of scape 10A), with an average of 40 per cent. With the growth of vivipars in succeeding years, without further production of flowers except on the small secondary scapes, the besom-like character is assumed, as noted in wild plants. The curves obtained by plotting the three elements according to their position on the scape are shown in the graph (Text fig. 2). The curves for the combined elements and for normal flowers approximate to that obtained from normal plants. In less close agreement is the curve for abnormal flowers, while the vivipar curve is distinct. The percentage increase of vivipars according to position on the scape is more strikingly shown in Text fig. 3.

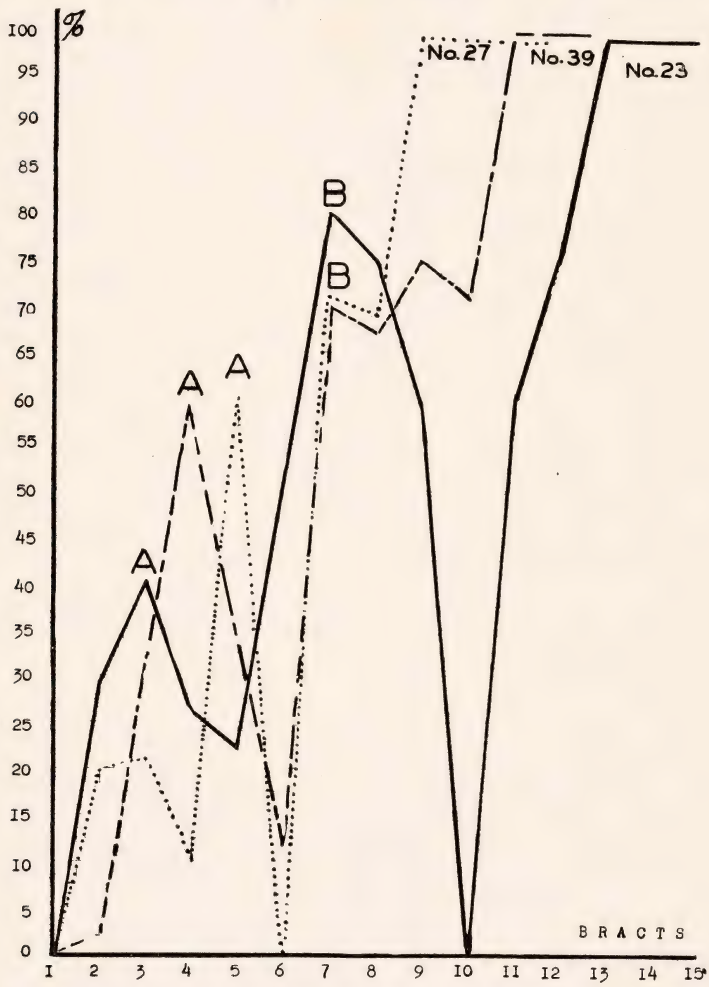

Fig. 4. Graph showing percentage of vivipars at each set up to the 15th bract on scapes from three plants. Note peaks and troughs.

The differences shown by the three scapes of plant 36 are noteworthy, 36B approaching normality. In scape 10A there were at bract 11 a number of congested vivipars, forming a mass that may have involved further bracts and sets. This scape, therefore, showed at an early stage the massing of the vivipars towards the summits of the scapes. We have found that the conduction of water and solutes through the persistent scapes is vigorous, and that the correlation between strong vivipars and root-formation, as against weak vivipars and formation of secondary scapes, is similar to that shown in the parent plants, and in wild plants. It was found possible to grow a good percentage of these vivipars on their removal from the scapes.

Williams (1904) failed to grow plantlets from his first scapes either because they were all weak, or probably because he planted them before aerial roots had had time to appear on any of them.

The percentage curves for individual scapes show noticeable parallelism in their peaks and troughs (fig. 4), but as these occur at different levels on the inflorescences, the percentage curve for all bracts is evened out. The consistent appearances of peaks A and B may be perhaps correlated with the weather conditions. Temperatures fell from the 1st to the 18th December, rose again till 3rd January, decreased till 15th January, rose again till 25th January, and decreased till 7th February. The temperatures during the succeeding period also showed fluctuations. There were thus two periods of warmer weather between three short periods of colder weather. The rainfall was more irregularly distributed, but the periods of lowest temperatures were drier than the others.

Correlation with weather seemed clear in the Henderson plants in one year. All plants, whether from seed or from vivipars, showed no sign of vegetative buds on scapes varying from 3 feet (*colensoi* type) to 9 feet in length (*tenax* type) on 8/1/41 at the end of a spell of very dry weather, but warm rains followed soon after, and by May all except one which most nearly approached *tenax* carried vivipars in upper parts of the scapes.

* * * *

Delay in the appearance of this paper enabled the junior author to see the Henderson plants this year after a longer drought, which, however, did not begin until January, the end of December having been cold and wet. Scapes had flowered and died on all the younger plants except one of *colensoi* type, which, by July, bore a tuft of viviparous fans, still mixed with flowers, indicating the late appearance of the scape. Old plants from the original "S" clump had not been checked in the production of vivipars. It is clear, however, that local factors are responsible for some extent for the yearly expression of vivipary in *Phormium*, but they cannot be as important as Schultz suggests for *Deschampsia flexuosa*. In an abstract which has just come to hand, Krotkov (1942) reports that Schultz (1939) experimented with a local form of this grass at the polar alpine Botanical Garden (Kola Peninsula), subjecting it to the action of a 10-hour day. As a result, both normal and shortened viviparous spikelets were induced. Schultz concludes that vivipary is apparently not congenital, "but a result of the interaction of the hereditary material constitution of the organism with definite conditions of existence." This would agree with the varying expression of vivipary we have observed in our plants, but it cannot be shown that the same changes have influenced garden specimens of either species, grown under the same conditions, or that comparable changes have affected the wild populations throughout the country: vivipary remains a very rare phenomenon in this genus. Nor does it explain why production of vivipars and abnormal flowers is so constant in the few wild examples discovered, nor why it is less marked in the hybrids most closely resembling *Phormium tenax*. Our observations show that the viviparous habit is inherited in our *Phormium* series, environmental conditions having only a secondary influence.

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